UNIVERSITY
OF LATVIA

Summary
of Doctoral Thesis

Astra Labuce

THE ECOLOGICAL IMPORTANCE OF MESOZOOPLANKTON DIVERSITY IN BRACKISH ECOSYSTEM AND ITS POTENTIAL IN ASSESSING THE ENVIRONMENTAL STATUS

Riga 2022

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SUMMARY OF DOCTORAL THESIS

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ANNOTATION

Zooplankton are an essential component in the pelagic food web, linking primary production to higher trophic levels, thereby playing a key role in the functioning of aquatic ecosystems. Here, in the dissertation, I analyze zooplankton diversity in relation to environmental factors. The extensive empirical information provides a general understanding of the dynamics of mesozooplankton and its diversity in the brackish water ecosystem, allowing to evaluate the potential in assessing the environmental status and identifying both opportunities and challenges for further work in this field. The main results are published in four SCOPUS publications. Unpublished data are also included in the dissertation. Mesozooplankton functional diversity was primarily controlled by abiotic factors if the habitat was homogeneous along the vertical dimension (as observed in the coastal regions of the Gulf of Riga). On the other hand, if a habitat was heterogeneous – divided into micro-habitats or niches – (as observed in the open waters of the Gulf of Riga), biotic factors, such as predation and competition, were decisive. The indicator describing the functioning of mesozooplankton (MSTS) showed convincing results in the open waters of the Gulf of Riga, where zooplankton diversity is largely controlled by biotic interactions. Therefore, I conclude that the dynamics of mesozooplankton diversity provide information on the pelagic food web in open water regions thus they can be used to assess the environmental status there. The functioning of coastal waters, on the other hand, is very different from that of open waters. The environmental status assessment based on the diversity parameters of mesozooplankton for the coastal environments is difficult due to the strong and variable influence of abiotic factors.

Key words: functional diversity; Baltic Sea; zooplankton; palagia; environmental status

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1. INTRODUCTION

A taxonomic classification is a traditional approach for describing biodiversity, most frequently using species richness – a widely used proxy for biodiversity (Gaston, 2000; Hamilton, 2005). However, it should be noted that biodiversity consists of three distinct parameters: taxonomic, functional and genetic diversity (Swenson, 2014; van der Plas, 2019), each of which characterizes a particular aspect.

Taxonomic diversity, although the most commonly described and studied, includes relatively least ecologically relevant information on population diversity (Swenson, 2014; Pomerleau *et al.*, 2015). Therefore, the taxonomy-centric approach alone usually cannot fully address ecological issues or assess environmental status, as it does not indicate changes in ecosystem functions (e.g., Petchey and Gaston, 2006; Barnett *et al.*, 2007; Litchman and Klausmeier, 2008; Pomerleau *et al.*, 2015; Hébert and Beisner, 2020).

Functional trait approaches ignore the species-centric view and characterize the set of traits and rates present in a population, providing ecologically more profound information on underlying mechanisms, such as strategies of the occurring species, community assembly, and ecosystem stability and resilience. Functional trait approaches are recommended as the main techniques for future studies on interactions between aquatic trophic levels, intra-group processes, causal link identifications, response assessments for, e.g., climate change or anthropogenic pressures, and to transcend ecosystems (Martini *et al.*, 2021).

Zooplankton are an essential component in the pelagic food web. They link primary production to higher trophic levels. Zooplankton in shallow systems (<50 m) and coastal regions are closely related to benthic processes. They are a food source for demersal meio- and macro-fauna (Rudstam *et al.*, 1992). A part of the zooplankton population spend a life stage in benthic habitat, e.g., in the form of benthic eggs (Lindley, 1990; Viitasalo and Katajisto, 1994; Walsh, 2013). Therefore, zooplankton have a key role in the aquatic environments in general, with particular emphasis on pelagic habitats (Barnett *et al.*, 2007; Sterner, 2009). Hence, their population parameters are included as water quality descriptors in Marine Strategy Framework Directive 2008/56/EC.

The functional diversity (FD) of zooplankton communities has been addressed in studies from different types of waterbodies worldwide (Gomes *et al.*, 2019), including the brackish Baltic Sea (Helenius *et al.*, 2017; Jansson *et al.*, 2020; Lokko *et al.*, 2017; Pecuchet *et al.*, 2020). FD of the Baltic zooplankton changes seasonally and along gradients of temperature, salinity, and depth (Helenius *et al.*, 2017; Jansson *et al.*, 2020). Also, zooplankton community composition and assembly in the Gulf of Riga is strongly driven by abiotic factors (Ojaveer *et al.*, 1998; Ikauniece, 2001; Kotta *et al.*, 2009). Hydrological conditions and climate variability are recognised as the main drivers shaping zooplankton FD in the area (Jansson *et al.*, 2020; Pecuchet *et al.*, 2020). Albeit, the effects of biotic interactions on zooplankton FD are left under-explored. Comprehension of processes behind zooplankton community assembly would provide a more in-depth understanding of the functioning of the food web and the ecosystem.

Pecuchet *et al.* (2020) described long-term, ecosystem-wide functional changes in the Gulf of Riga. However, the study was limited to copepods, thus the results cannot be extrapolated to the whole zooplankton community. In brackish waters, also rotifers and cladocerans significantly affect primary producers (Calbet, 2008) and serve as a linkage to the microbial food web (Johansson *et al.*, 2004; Motwani *et al.*, 2018). They provide substantial support for ecosystem production and functioning, especially in shallow, eutrophied, and coastal regions (Snoeijs-Leijonmalm, 2017).

The aim of the study: To determine mesozooplankton diversity in Latvian marine waters in order to evaluate its ecological importance and the potential in assessing the environmental status, thereby providing new knowledge about the functioning of the brackish water ecosystems.

Objectives:
1. To determine long-term dynamics of mesozooplankton taxonomic and functional diversity;
2. To identify environmental parameters (abiotic and biotic) affecting mesozooplankton functional diversity;
3. To elucidate the effects of benthic-derived recruitment on mesozooplankton diversity;
4. To evaluate the ecological importance of mesozooplankton functional diversity in the study area.

Publications:

(I) Labuce A., Strake S. (2017) An overview of *Synchaeta* Ehrenberg, 1832 (Rotifera: Monogononta: Synchaetidae) species in the Eastern Gotland Basin, Baltic Sea, with complementary characteristics for the trophi of *S.fennica* Rousselet, 1902 and *S.monopus* Plate, 1889. *Proceedings of the Estonian Academy of Sciences* 66(3):287-294. Author's contribution: 95%. DOI: 10.3176/proc.2017.3.06

(II) Labuce A., Ikauniece A., Strake S., Souissi A. (2018) Survey of Presence of non-indigenous *Eurytemora carolleea* in the Gulf of Riga (Baltic Sea) Five Years after its First Discovery. *Proceedings of the Latvian Academy of Sciences. Section B. Natural, Exact, and Applied Sciences* 72(4):230-235. Author's contribution: 80%. DOI: 10.2478/prolas-2018-0032

(III) Labuce A., Dimante-Deimantovica I., Tunens J., Strake S. (2020) Zooplankton indicator-based assessment in relation to site location and abiotic factors: a case study from the Gulf of Riga. *Environmental Monitoring and Assessment* 192, 147. Author's contribution: 70%. DOI: 10.1007/s10661-020-8113-9 Erratum: Labuce *et al.* (2020*a*)

(IV) Labuce A., Ikauniece A., Jurgensone I., Aigars J. (2021) Environmental Impacts on Zooplankton Functional Diversity in Brackish Semi-Enclosed Gulf. *Water (Switzerland)*, 13(14): 1881. Author's contribution: 80%. DOI: 10.3390/w13141881

Scientific novelty

Studies on mesozooplankton diversity conducted in the Eastern Baltic Sea, including Latvian marine waters heretofore have focused on individual or several taxonomic groups and their variation under abiotic pressures. Here, I present the first study which (i) identifies long-term changes in mesozooplankton taxonomic and functional diversity, considering all groups (copepods, cladocerans, rotifers, meroplankton) and (ii) analyzes the ecological importance of mesozooplankton diversity in the ecosystem of the Gulf of Riga, taking into account effects of biotic factors (predation, competition, bentho-pelagic coupling). In the dissertation, I have analysed national monitoring data to obtain long-term dynamics of mesozooplankton taxonomic and functional diversity in relation to environmental factors (**paper III**, **IV**), and also I have conducted three case studies. Two of the case studies scrutinize the taxonomic diversity focusing on hard-to-identify mesozooplankton species (**paper I**, **II**), whereas the third case study investigates bentho-pelagic coupling in the Gulf of Riga (**V** - unpublished). The extensive empirical information provides a general understanding of the dynamics of mesozooplankton and its diversity in the studied area, allowing to evaluate the potential in assessing the environmental status, and identifying both opportunities and challenges for future work.

Aspects of environmental policy

In the field of marine environmental policy, the most relevant document binding on the Baltic Sea Region is Marine Strategy Framework Directive 2008/56/EC (MSFD), which strongly emphasizes the need to reduce impacts on natural marine resources to ensure the long-term functioning of the ecosystem. MSFD aims to contribute to the achievement or maintenance of good environmental status in European regional seas. MSFD stipulates that environmental status assessment must be conducted based on indicators that characterize defined descriptors (Annex I to the MSFD). This study is directly relevant to the assessment of Descriptor 1 ”Biological diversity is maintained” (MSFD D1), and partly relevant to Descriptor 2 (non-indigenous species; MSFD D2), Descriptor 4 (marine food webs; MSFD D4) and Descriptor 5 (eutrophication; MSFD D5).

Baltic Sea Action Plan (BSAP) is a regional agreement between all contracting parties of Baltic Marine Environment Protection Commission (HELCOM), including Latvia. BSAP contains a section on biodiversity and nature conservation, which states that water quality must be promoted in a way that ensures the integrity, structure and functioning of the ecosystem, as well as thriving and balanced plant and animal communities. European Union Strategy for the Baltic Sea region and the European Green Deal also impose an obligation to preserve and restore ecosystems and biodiversity. However, a comprehensive understanding of processes and their interactions is needed to preserve and restore; this dissertation provides information on the functioning of the pelagic habitat, supplementing the knowledge-base about the brackish water ecosystems.

Practical significance

MSFD states that every country of the European Union, including Latvia, must assess the environmental status of its territorial marine waters every six years. This dissertation summarizes my work done in the period from 2014, which has facilitated the progress of such an assessment. It details the characteristics of the zooplankton population data and explains the methodology for calculating zooplankton indicators and diversity parameters. Also, the results of this dissertation, which analyze the dynamics of the mesozooplankton community within the ecosystem context, provide information relevant for the implementation of ecosystem-based management, e.g. for the assessment of pelagic food web (MSFD D4) and its functioning. In addition to the above, the results can serve as the basis for further steps to promote the development of a bioeconomy based on marine resources in Latvia. The sustainable growth of the marine bio-economy is directly linked to the wise use of resources at lower webs, as the impact of traditional fisheries on the ecosystem needs to be significantly changed.

Dissemination of the results:

1) 78th International Scientific Conference of the University of Latvia, Rīga, Latvia. 24.01.2020., oral presentation (in Latvian). Labuce A. "Zooplankton functional diversity and its affecting factors in the Gulf of Riga".

2) 77th International Scientific Conference of the University of Latvia, Rīga, Latvia. 01.02. 2019., oral presentation (in Latvian). Labuce A., Strāķe S., Tunēns J. "Use of zooplankton population parameters (mean size and total biomass) as an indicator for assessing the impact of pelagic food webs and eutrophication: application of HELCOM core indicator MSTS in the Gulf of Riga".

3) Use of molecular-genetic and morphological methods to study the taxonomy, phylogeny, bio-geography, and ecology of *Eurytemora* species, Saint-Petersburg, Russia. 13.-17.05.2019., oral presentation (in English). Labuce A., Ikauniece A., Strake S., Souissi A. "Survey of Presence of non-indigenous *Eurytemora carolleea* in the Gulf of Riga (Baltic Sea) Five Years after its First Discovery".

4) 76th International Scientific Conference of the University of Latvia, Rīga, Latvia. 30.01.2018., oral presentation (in Latvian). Labuce A., Strāķe S. "Differences in the population dynamics of the dominant copepods in the Gulf of Riga in relation to their spawning strategy".

5) 3rd ICES/PICES Early Career Scientist Conference "Climate, Oceans and Society: Challenges & Opportunities", Pusan, South Korea. 30.05.-2.06.2017., oral presentation (in English). Labuce A., Strake S. "Effect of variability in environmental conditions on Baltic Sea Calanoid Copepod egg bank and recruitment".

6) 74th Scientific Conference of the University of Latvia, Rīga, Latvia. 01.02.2016., oral presentation (in Latvian). Labuce A., Strāķe S., Ikauniece A. "Copepod *Eurytemora affinis* in the Gulf of Riga".

7) Plankton Resting Stage Workshop "Geological, Ecological and Evolutionary Perspectives", Tvärminne zoological station, Hanko, Finland. 5.-8.10.2015., poster (in

English). Labuce A. “Effect of variability in environmental conditions on Baltic Sea Calanoid Copepod egg bank and recruitment. Preliminary results”.

8) 10th Baltic Sea Science Congress, Rīga, Latvia. 15.-19.06.2015., poster (in English). Labuce A., Strake S. “Seasonal and spatial occurrence and development of zooplankton benthic eggs under various environmental conditions in sediments of the Gulf of Riga, Baltic Sea”.

The dissertation includes results obtained in the following projects:

- Project No.1-08/145/2017 funded by Latvian Environmental Protection Fund Administration (LVAFA) “Development of pelagic indicators for the assessment of the environmental status of Latvian marine waters”, 2016-2017
- Project funded by European Maritime and Fisheries Fund via Ministry of Environmental Protection and Regional Development (contract No.IL/106/2017) „Improving the knowledge of the state of the marine environment” project No. 17-00-F06803-000001, 2017-2022
- National Research Program 2014-2017 ”The value and dynamic of Latvia’s ecosystems under changing climate”, 2014-2017
- Fund of the ”Osmosis” program of the Ministry of Education and Science of the Republic of Latvia and the Ministry of Foreign Affairs of France (Contract No. 10-13/11)

Thesis for defence:

- Parameters of mesozooplankton diversity (species number, abundance of functional groups, mean size and total stock, functional diversity indices) show different long-term dynamics between coastal and open water regions;
- Biotic interactions (predation, competition) are decisive for the variability of mesozooplankton functional diversity in the Gulf of Riga during the summer;
- Mesozooplankton diversity is linked to the hatching of benthic eggs;
- Parameters of mesozooplankton functional diversity assess the environmental status of pelagic habitat in the study region.

2. MATERIALS AND METHODS

2.1. Study area

The study area is the territorial marine waters of Latvia, including the coastal Eastern Gotland Basin and coastal and the Gulf of Riga (Figure 2.1, Table 2.1). However, the study focus is placed on the ecosystem of the Gulf of Riga. It is subjected to a seasonal cycle with a convection period from autumn to spring and a stratification period during summer (Snoeijs-Leijonmalm and Andrén, 2017). The Gulf of Riga is a shallow (mean depth of 27 m) brackish waterbody. It is highly affected by freshwater runoff (Andrushaitis, 1995), resulting in a NW-ward salinity gradient (up to 7.0 PSU).

2.2. Sampling and analysis of mesozooplankton (papers I, II, III, IV)

Mesozooplankton samples were collected using WP-2 net (mesh size 100 µm) (**paper II**, **III**, **IV**), except for the study conducted in Liepaja Port (**paper I**), where Apstein-type plankton net (mesh size 56 µm; opening 0.09 m^2) was used. All mesozooplankton samples were preserved in 4% buffered formalin, handled and analysed following HELCOM COMBINE recommendations (HELCOM, 2017), except for the studies described in **paper I** and **II**.

In the study described in **paper I**, after identification of the genus *Synchaeta* based on the body's external morphological features, individuals were placed in a small drop of water on a microscope slide (76×26 mm) covered with a coverslip (18×18 mm). Then a drop of household bleach (NaOCl < 5%) was added next to the coverslip ensur-

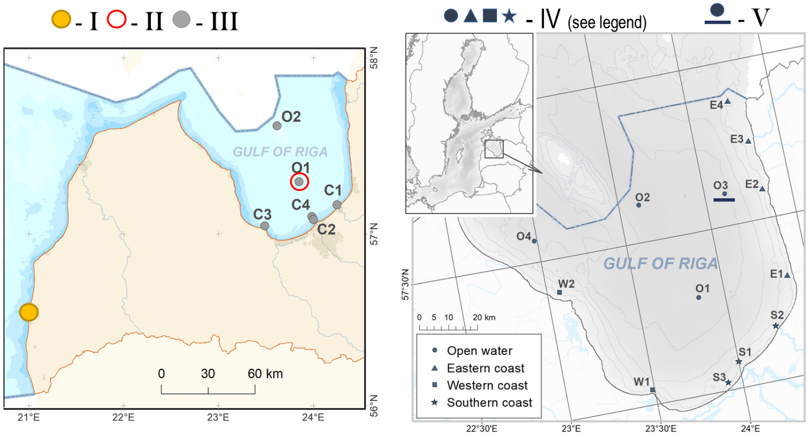


Figure 2.1. Map of the study area. I - Case study on diversity of rotiferans in the Liepaja Port waters; II - Case study on inspection of non-indigenous *Eurytemora carolleeae* presence in the Gulf of Riga; III - testing of MSTS indicator in the Gulf of Riga; IV - study on long term dynamics of mesozooplankton functional diversity in the Gulf of Riga; V - study on bentho-pelagic coupling in open waters of the Gulf of Riga (unpublished).

ing they were both in contact and bleach was drawn under the coverslip. After a few minutes, all soft tissues dissolved and only the hard parts of the mastax – trophi left. The internal structure of trophi is the most significant characteristic in Rotifera species identification (De Smet, 1998; Obertegger *et al.*, 2006). In the study described in **paper II**, after the identification of *Eurytemora* genus, 75 females and 75 males were selected; 25 from each season: spring (May), summer (August), autumn (November). Three morphometric indices (Sukhikh *et al.*, 2013) were used to distinguish between *E.affinis* and *E.carolleeae*: length/width of the caudal rami , anterior/posterior sides of the genital segment and length/width of the exopodite first segment of the 5th swimming leg.

Table 2.1

Characteristics of stations included in the dissertation. No III - assigned numbering in **paper III**; No IV - assigned numbering in **paper IV**; Mon. no – numbering of Latvian National monitoring stations. Water-type: 1 – open waters, 2 – coastal waters, 3 – transitional waters.

No III	No IV	Mon. no	Coord.	Depth (m)	Water-type
O1	O1	119	57°18'N 23°51'E	44	1
O2	O2	121	57°37'N 23°37'E	56	1
	O3	121A	57°36'N 24°07'E	43	1
	O4	142	57°34'N 23°58'E	42	1
C2	S1	165	57°05'N 24°01'E	12	3
C1	S2	163	57°10'N 24°15'E	12	3
	S3	167	57°02'N 23°55'E	12	3
C3	W1	170	57°03'N 23°29'E	12	2
	W2	172	57°24'N 23°04'E	12	2
	E1	162	57°19'N 24°22'E	12	2
	E2	160	57°36'N 24°20'E	12	2
	E3	159	57°46'N 24°15'E	12	2
	E4	158	57°53'N 24°15'E	12	2
C4		101A	57°06'N 23°59'E	22	3

2.3. The study on MSTS indicator (paper III)

"Mean Size and Total Stock" indicator (MSTS) is used for environmental assessment in the open waters of the Baltic Sea. It is a two-component indicator combining zooplankter mean size (MS, µg ind^{-1}) and total stock (TS, ind or mg per m^3). MSTS-based environmental assessment analyses long-term dynamics of the lower cumulative sum of z-scores; if it decreases below -5, the environmental status is considered "bad". Here, the concept of MSTS (as described in Gorokhova *et al.*, 2016; HELCOM, 2018) is tested in the Gulf of Riga aiming to evaluate differences in its performance between open and coastal waters. Also, I have developed MSTS indicator calculation tool (published on GitHub: ./helcomsecretariat/ZooplanktonMeanSizeTotalStock) for easier and more transparent use of MSTS indicator.

MSTS relation to temperature, salinity and runoff analysed using generalized additive modelling (GAM) function from "mgcv" package in the R environment (R Core

Team, 2020). Data on temperature and salinity obtained from long-term database of Latvian Institute of Aquatic Ecology (LHEI), whereas data on annual runoff were obtained from the database (`https://www.meteo.lv/en/`) maintained by Latvian Environment, Geology and Meteorology Centre.

2.4. Estimation of mesozooplankton functional diversity (paper IV)

Functional diversity (FD) of the summer mesozooplankton community was estimated based on categorized trait values (Table 2.2). Hierarchical agglomerative clustering was applied to define functional groups of zooplankton communities. The agglomeration method and optimal cluster number were identified by evaluating cluster validation statistics (package ”fpc” (Hennig, 2020)).

Four FD indices (functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis)) were calculated by means of the *dbFD* function from the ”FD” package (Laliberté and Legendre, 2010; Laliberté *et al.*, 2014) using R v3.6.1. Gower's (Gower, 1971; Podani, 1999) dissimilarity between species based on traits (Table 2.2) were calculated and used as an input value. In further analysis, only standardised effect sizes of FRic, FDis, and FDiv indices were used, yielding SESFRic, SESFDis, and SESFDiv. FEve were not adjusted (following Mason *et al.* (2013)) and used as calculated by the *dbFD*.

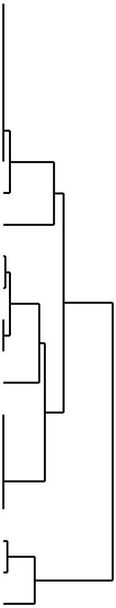
Multiple Factor Analysis (MFA) was used to identify spatial environmental gradients of the Gulf of Riga to define differences in the study areas (open waters, eastern coastal area, western coastal area, and southern coastal area) and to describe co-varying environmental parameters. MFA was conducted using the ”FactoMineR” package (Lê *et al.*, 2008). GAM was applied (”INDperform” package, Otto *et al.*, 2020) to evaluate mesozooplankton FD responses to variations in hydrological parameters (SST, SSS), cyanobacterial dominance (cyano:other), dynamics of zooplankton functional groups, and predation pressure (herring spawning biomass (her-totSPbio), herring total stock biomass (her-totBio), and the number of herring recruitment (her-Rec)). A non-random 9:1 train-test split was conducted, and *normalised root mean square error* (nrmse) was calculated for every significant relationship. The response was assessed on data from 1993–2014, whereas the test data (used for nrmse calculation) were from 2015–2017. Herring population data were obtained from an annual report by the Baltic Fisheries Assessment Working Group (ICES, 2018).

2.5. Estimation of benthic-derived recruitment (V-unpublished)

Six sediment samples from station 121A (Figure 2.1) were used in every hatching experiment (in total three: May, August, November). Surface 2 cm of sediments were collected with a corer (diameter 8 cm). Each sediment sample, immediately after collection, was placed in 500mL container (plastic bucket with a lid) and carefully, without clouding poured with filtered (Whatman GF/C class fiberglass filter with a pore size of 1.2 µm) water from the Gulf of Riga (≈300 mL). In the refrigerated boxes, the samples were transported to the laboratory, where they were placed in a temperature-controlled room at 7ºC. Three samples were aerated and three samples were not aerated. The incubation lasted for 2 weeks. Twice a week, water was drained from each sample and poured with filtered (Whatman GF/C class fiberglass filter with a pore size of 1.2 µm) water from the Gulf of Riga, which was stored at the same temperature as the samples. The water drained from the samples was filtered through a sieve (mesh size 50 µm) and analyzed immediately, without fixation using transmitted light microscopy. Between every water change there were at least 72 hours. All hatched organisms were counted and identified.

Table 2.2

Mesozooplankton functional traits and their values. All traits are categorical. FM (feeding mode): A, ambush; F, feeding current; C, cruising/raptorial; M, mixed feeding; ML (mean length): 1, ≤0.40 mm; 2, 0.41–0.80 mm; 3, 0.81–1.20 mm; 4, 1.21–1.60 mm; 5, 1.61–2.00 mm; PS (prey size): 1, ≤0.010 mm; 2, 0.011–0.050 mm; 3, >0.050 mm; TG (trophic group): H, herbivore; C, carnivore; O, omnivore; HS (selectively predated by herring; categories defined based on a study by Livdāne *et al.* (2016): 0, not selectively predated; 1, moderately selected; 2, highly selected. The dendrogram is based on Gower's dissimilarity using 'complete linkage' agglomeration. References - in footnotes. Table from Labuce *et al.* (2021).

Func. group	**Abbreviation**	**FM**	**ML**	**PS**	**TG**	**HS**	**Dendrogram**
G1	KerCoch	*F*[a]	1[b]	1[a]	*H*[a]	0	
	KerQua	*F*[a]	1[b]	1[a]	*H*[a]	0	
	KerCruc	*F*[a]	1[b]	1[a]	*H*[a]	0	
	Amph	*F*[c]	1[d]	1[c]	*H*[c]	0	
	Poly	*F*[a]	1[e]	1[e]	*H*[e]	0	
	Biv	*F*[f]	1[g]	1[f]	*H*[g]	0	
	Bos	*F*[h]	1[d]	1[i]	*H*[h]	1	
G2	Cycl	*A*[j]	2[d]	2[i]	*C*[k]	0	
G3	Pleo	*M*[lm]	3[d]	2[lm]	*C*[lm]	1	
	Evad	*M*[lm]	4[d]	2[lm]	*O*[lm]	1	
	AcSpp	*M*[j]	3[j]	2[i]	*O*[n]	0	
	AcLon	*M*[j]	3[j]	2[i]	*O*[n]	0	
	Tem	*F*[j]	4[j]	2[i]	*O*[o]	0	
G4	SySpp	*C*[a]	1[p]	1[a]	*O*[a]	0	
	SyBal	*C*[a]	1[p]	1[a]	*O*[a]	0	
	CalN	*C*[r]	1[r]	1[i]	*O*[s]	0	
	CycN	*C*[r]	1[r]	1[i]	*O*[k]	0	
G5	Limn	*C*[t]	5[j]	3[i]	*C*[t]	2	
	Cerc	*C*[u]	5[u]	3[i]	*C*[u]	1	
	Eury	*C*[j]	4[j]	2[i]	*O*[u]	2	

[a] Ruttner-Kolisko (1974) [b] Berzins (1960) [c] Pansch *et al.* (2013) [d] Telesh and Heerkloss (2004)
[e] Burckhardt *et al.* (1997) [f] Arapov *et al.* (2010) [g] Raby *et al.* (1994)
[h] Sommer and Sommer (2006) [i] Hansen *et al.* (1994) [j] Brun *et al.* (2017) [k] García *et al.* (2011)
[l] Egloff *et al.* (1997) [m] Katechakis and Stibor (2004) [n] Tiselius (1989) [o] Gentsch *et al.* (2009)
[p] Hollowday (2002) [r] Titelman and Kiørboe (2003) [s] Stoecker and Egloff (1987) [t] Warren (1985)
[u] Rivier *et al.* (1998) [u] Aladin and Panov (2000) [u] Revis *et al.* (1991)

3. RESULTS AND DISCUSSION

3.1. Diversity of mesozooplankton (papers I, II, IV)

Taxonomic diversity of mesozooplankton varied seasonally in both the Gulf of Riga and the coastal Eastern Gotland Basin (EGB). The highest number of species was observed from July to September, with slightly higher values in the Gulf of Riga (8 species on average in August) than on the coastal EGB. However, these estimates most likely are underestimated due to the presence of difficult-to-identify taxa. For example, illoricate rotifers from the *Synchaeta* genus (Hollowday, 2002) and a complex of cryptic *Eurytemora* species (Lee and Frost, 2002) are often pooled at a higher taxon level.

Identification of *Synchaeta* at a genus level is widely used in the Baltic Sea region (e.g., Ojaveer *et al.*, 1998; Dippner *et al.*, 2000; Kornilovs *et al.*, 2004) as identification to species level requires morphological analysis of every individual. **Paper I** of this dissertation focuses on the identification of *Synchaeta* to species level in order to assess their diversity in the region. In the result, altogether four species were found in the samples from coastal EGB (Port of Liepaja). They were *S.baltica*, *S.fennica*, *S.monopus* and *S.triopthalma*, of which the latter was found for the first time in the territorial waters of Latvia. The same method of *Synchaeta* identification has been used in the analysis of zooplankton samples in the Gulf of Riga (unpublished). Three species (*S.baltica*, *S.fennica*, *S.monopus*) that are typical to the Baltic Sea were found in the Gulf of Riga, as well as one unidentifiable species that morphologically is similar to *S.vorax*, but its trophi structure does not fit the description. Consequently, estimated diversity of *Synchaeta* species remains incomplete and would require in-depth research, including both electron-microscopy for trophi analysis and molecular methods for species identification. In total, eleven *Synchaeta* species have been reported found in the Baltic Sea region (Berzins, 1960; Kutikova, 1970; Hollowday, 2002; Telesh and Heerkloss, 2002; Telesh *et al.*, 2009).

Paper II investigates the presence of non-indigenous *Eurytemora carolleeae* in the Gulf of Riga. *Eurytemora carolleeae* morphologically is very similar to the native *E.affinis*, hence differentiation between them was made based on morphometric indices (see Section 2.2.). The obtained results show that, contrary to the expected of Sukhikh *et al.* (2013), *E.carolleeae* has not succeeded in establishing an independent population in the Gulf of Riga in five years since its first finding in 2008. However, considering the high reproductive rates (Pierson *et al.*, 2016) and longer lifetime of *E. carolleeae* (Beyrend-Dur *et al.*, 2009), the accurate identification of *Eurytemora* species should continue to receive increased attention in the region.

From a long-term perspective, the number of mesozooplankton species has increased in the Gulf of Riga between the mid-1990s (an average of six species in 1994) and the early 2000s, when an average of 10-13 species were found (Figure 3.1A). The increase was followed by a gradual decrease (an average of 7 species in 2006). Since 2008, the average number of mesozooplankton taxa in the coastal regions remained stable (approx. 7), while the average number of species in the open waters varied in the

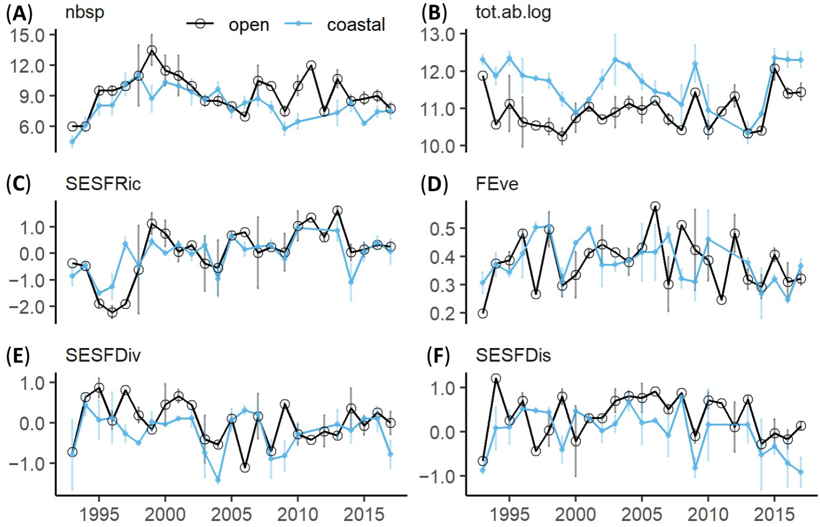


Figure 3.1. Long-term dynamics of summer mesozooplankton communities in open and coastal areas (mean of western, eastern, and southern coastal area) of the Gulf of Riga. Error bars represent the standard deviation of the mean. (A) nbsp — number of observed taxa; (B) tot.ab.log — natural log of total abundance; (C) SESFRic — functional richness; (D) FEve — functional evenness; (E) SESFDiv — functional divergence; (F) SESFDis — functional dispersion. Figure from Labuce *et al.* (2021).

range from 7 to 12. At the same time, the total abundance of mesozooplankton showed the opposite trend; in coastal waters it was higher than in open waters, but also it was highly variable (Figure 3.1B).

In the study described in **paper IV**, analyzing the period from 1993 to 2017, it was found that herbivorous filter-feeders (func.group G1) dominated the mesozooplankton community in both coastal and open waters of the Gulf of Riga. Small-sized omnivores (func.group G3) were the second most common group, whereas large-sized omnivores (func.group G4) and taxa defined as the main herring prey (func.group G5) were substantially less abundant (Figure 3.2).

Long-term dynamics of functional diversity (FD) indices show that distinct FD characteristics display different patterns and trends (Figure 3.1C-F). SESFRic was almost identical in coastal and open waters (Figure 3.1C). It showed the lowest values in the early 1990s, which coincides with the period when the lowest number of mesozooplankton species was found in the Gulf of Riga (Figure 3.1A). SESFRic and the number of present species are positively related (e.g., Mason *et al.*, 2005), so it could be assumed that SESFRic provides information on both functional richness (*"how many traits are present?"*) and dynamics of species number (*"is the number of present species increasing?"*) concurrently.

FEve varied annually in both open and coastal areas without an evident trend (Fig-

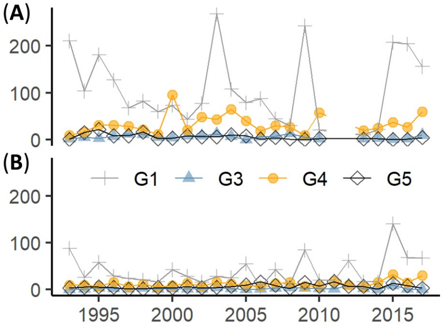


Figure 3.2. Long-term abundances of mesozooplankton functional groups in the Gulf of Riga coastal (A) and open (B) areas. Values shown as 1000 ind m^{-3}. Functional groups (G1, G3, G4, and G5) defined in Table 2.2. Figure from Labuce *et al.* (2021).

ure 3.1D). SESFDiv values were high during the late 1990s and early 2000s, indicating that the mesozooplankton community consisted of functional groups that were more distinct from one another (located closer to the extreme ends of the trait space). After the year 2002, the distinction between functional groups slightly decreased implying that the abundant traits are becoming more similar (Figure 3.1E). Such dynamics of SESFDiv was observed both in coastal and open waters of the Gulf of Riga.

Based on SESFDis values, mesozooplankton communities in coastal areas of the Gulf of Riga appeared functionally less dispersed than those in open areas (Figure 3.1F). However, annual dynamics were similar between area type, noting that the responses to disturbances were most likely analogous. From 2003 to 2008, SESFDis showed continuously high values indicating the most functionally diverse period (considering the traits included in the analysis – see Table 2.2).

Referring to the observed increase in the number of mesozooplankton species after the year 2000, it should be noted that several non-indigenous species were first found in the Baltic Sea in the 1990s, as well as in the early 2000s. Some of the newcomers, such as *Cercopagis pengoi*, *Evadne anonyx* and polychaeta *Marenzelleria viridis*, have a direct effect on mesozooplankton population and its structure.

Cladoceran *C. pengoi*, detected in the Gulf of Riga in 1991 (Ojaveer *et al.*, 1999), has an evident impact on the pelagic food web as it competes with planktivorous fish for larger mesozooplankton prey (func.groups G3 and G5) and graze upon small-sized zooplankters (func.groups G1 and G4). So far, it has been established that the invasion of *C.pengoi* in the Gulf of Riga has contributed to the decline in abundance of cladocerans *Bosmina* and *Pleopis* and copepod *E.affinis* (Ojaveer *et al.*, 2004; Kotta *et al.*, 2006; Einberg *et al.*, 2020). But there has also been a small increase in abundance of copepod nauplii in the Gulf of Riga after the *C.pengoi* invasion (Einberg *et al.*, 2020). At the same time, herring *Clupea harengus membras*, ninespine stickleback *Pungitius pungitius*, common bleak *Alburnus alburnus* and European smelt *Osmerus eperlanus* feed on *C.pengoi* (Gorokhova *et al.*, 2004; Ojaveer *et al.*, 2004; Kotta *et al.*, 2006).

3.2. Performance of the indicator MSTS in the Gulf of Riga (paper III)

The parameters of MSTS indicator (mean size (MS) and total stock (TS)) are displaying the functioning of the pelagic food web based on the mesozooplankton population and its structure. MS characterises fish food quality, whereas TS represents the overall community size, with higher values reflecting better food availability for planktivorous fish and higher grazing pressure on the primary produces (potential of mitigating eutrophication effects). In **paper III**, The testing of the MSTS indicator in the Gulf of Riga is described. MSTS indicator was developed to assess open water areas (HELCOM, 2018), but here an analysis of its potential as an indicator in the coastal and transitional waters was evaluated as well.

MSTS mean values of the assessment period showed good environmental status (GES) for both parameters at all sampling sites (Table 3.1). However, when the inter-annual variability (confidence intervals) was considered, five of nine cases showed a 99% possibility of sub-GES, indicating overall low confidence in the mean, especially in the coastal sites.

Table 3.1

Mean size and total stock (MSTS)-based assessment for period 2012–2017 of the Gulf of Riga (GoR). For sites (St.) location, see Table 2.1. MS - mean zooplankton size (individual wet weight; µg ind^{-1}), TZA - total zooplankton abundance (1000 ind m^{-3}), TZB - total zooplankton biomass (mg m^{-3}). Sub-GES cases are bolded. Table from Labuce *et al.* (2020*a*).

St.	GES threshold			Assessment (2012-2017)	
	MS	TZB	TZA	vid	$_{L}CI99\%$
163	2.29	303	93	GES	**nGES**
165	2.39	283	87	GES	**nGES**
170	2.02	108	26	GES	GES
101A	1.23	102	19	GES	GES
coastal	2.54	258	58	GES	**nGES**
119	2.90	155	36	GES	**nGES**
121	2.81	77	19	GES	GES
open	2.89	130	32	GES	GES
GoR	3.09	209	48	GES	**nGES**

The Gulf of Riga is a shallow waterbody; hence, coastal processes are as equally relevant for ecosystem functioning as off-shore ones. Arula *et al.* (2016) described early larvae of the Gulf of Riga herring being the key stage for the overall success of the recruitment, pointing to the importance of feeding conditions at coastal locations – the main feeding grounds for herring larvae. Considering the typical diet of herring larvae that includes copepod nauplii and eggs of planktonic organisms, sometimes also copepodites (Ojaveer, 2017), which are overall, small-sized prey, a recommendation would be to include only the TS parameter, more precisely the total number of zooplankton individuals (TZA) in the assessment of MSTS conducted in coastal waters.

Use of abundance (TZA) data will avoid the potential misconception that TZB might cause, when assessing a low-numbered population prevailed by large-bodied organisms – a community not suitable for herring larvae.

3.3. Mean Size and Total Stock relation to environmental factors (paper III)

A comparison of MSTS results between coastal areas and open waters revealed different long-term trends. While TS decreased steadily in the period 2009–2014 in coastal stations 163 and 165 (Figure 3.3a-b), analogous changes were absent in coastal st. 170 and 101A (Figure 3.3c–d). Despite the visual similarity of CuSum (cumulative sum of z scores) patterns between coastal st. 163 and 165 (where TS decreased) and mean values of the coastal area and the Gulf of Riga in general (Figure 3.3), none of the tested environmental factors explained variations in TS or MS at st. 163 and 165. The south-eastern coastal part of the Gulf of Riga (where st. 163 and 165 are located) is affected by factors directly related to river runoff, and it is regarded to be

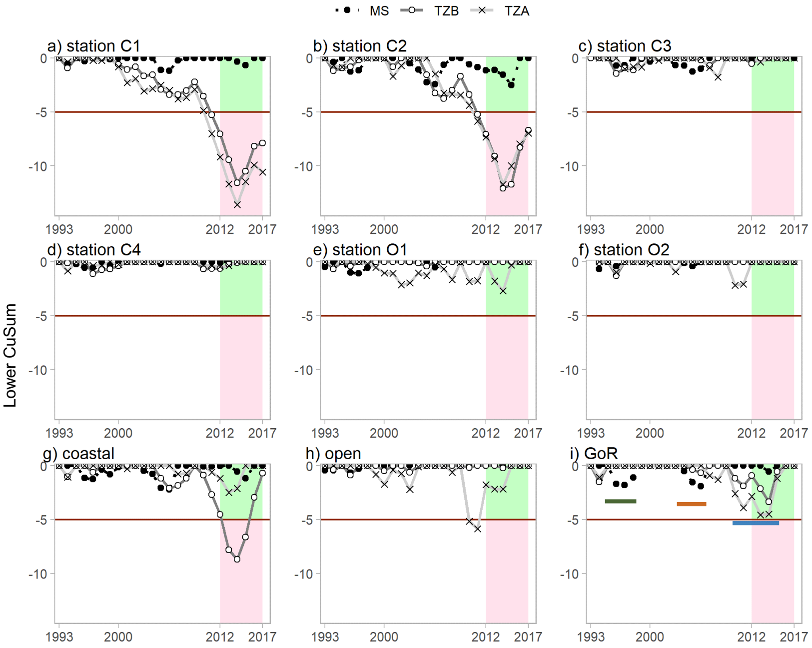


Figure 3.3. Lower cumulative z-value sum control (Lower CuSum) charts included in Mean Size and Total Stock (MSTS) indicator-based assessment of the Gulf of Riga. Station name abbreviations described in Table 2.1. MS - mean zooplankton size (individual wet weight), TZA - total zooplankton abundance, TZB - total zooplankton biomass. Threshold value of Lower CuSum (horizontal red line) = −5. Line segments in subgraph i) show periods when Lower CuSum for mean of the Gulf of Riga was decreased (from left: 1995–1998; 2003–2006; 2010–2014). Figure from Labuce *et al.* (2020*b*).

turbid transitional waters. Most likely, a single factor cannot be defined as the main influencing factor using our approach (i.e, GAM) due to dynamic processes in the area.

At stations further away from the area of direct impact of river runoff, a statistically significant relationships were found between MSTS parameters and both temperature and salinity. The results showed that TS (TZA in particular) is affected by salinity during the MSTS test period in both transitional waters (st. 101A) and open water stations, and also on average in the Gulf of Riga (TZB un SSS: $R_{sq} = 0.24$, $p = 0.012$; TZA un SSS: $R_{sq} = 0.30$, $p = 0.005$), while the MS parameter is related to temperature changes (MS un SST: $R_{sq} = 0.32$, $p = 0.035$).

However, combining results of both GAM and CuSum, partly explained the CuSum dynamics also in st. 163 and 165 (Figure 3.3a-b), coinciding with already established relationships. Both downward trends of MS (Figure 3.3i) were initiated after several consecutive years when mean surface water temperature in summer was below long-term average (1995–1998 and 2003–2006), whereas TS responded to continuously low values in salinity (2010–2014).

Detected relationships demonstrate the potential changes in MSTS parameters that would enhance under climate change. The latest projections predict a significant increase in water temperature and a decrease in salinity (mainly due to increase in runoff) for the Baltic Sea region, including the Gulf of Riga (Von Storch *et al.*, 2015). According to Skudra and Lips (2017), the potential thermohaline effects for the Gulf of Riga in the case of such change are stronger stratification conditions (potentially leading to oxygen depletion in the deeper areas) and an increase in nutrient loads intensifying eutrophication effects. Both of these alterations will affect MSTS parameters. A decrease of oxygen concentration would limit *Limnocalanus macrurus* recovery (Kane *et al.*, 2004). *Limnocalanus macrurus* is the largest-bodied Baltic Sea copepod and its population size has a direct effect on the value of the MS parameter. Moreover, oxygen depletion would also unpredictably affect zooplankters that rely on bottom-derived recruitment, as oxygen is essential for hatching of benthic eggs and further animal development (Broman *et al.*, 2015).

Considering all of the above, it can be concluded that as a result of climate change the zooplankton population structure in the Gulf of Riga will be affected. However, as the parameters of the MSTS indicator are not related to specific taxa or functional groups, but robustly reflect the ability of the zooplankton population to transfer energy from producers to higher trophic levels, its potential to characterize and assess pelagic environmental status is high even under changing environmental conditions.

3.4. Mesozooplankton FD in relation to environmental factors (paper IV)

3.4.1. *Spatial variability*

FD indices and dynamics of zooplankton functional groups, in contrast to the MSTS indicator, characterize specific groups of zooplankters, providing more in-depth information on the processes within the zooplankton community. According to the result of multi factorial analysis (MFA), the Gulf of Riga open waters are notably different from all of the studied coastal areas based on differences in hydrological conditions, cyanobacterial dominance (cyano:other ratio), the abundance of mesozooplankton functional groups, and mesozooplankton FD indices (SESFRic, FEve, SESFDiv, and SESFDis). Also, the results of MSTS indicator displayed differences in coastal and open water zooplankton communities (see Section 3.2.).

Surface 0-10 m temperature (SST), the main driver of Dim1 of MFA, and cyano:other ratio, the main driver of Dim2, showed evident increasing values from coastal areas to open waters (Figure 3.4). The salinity gradient, which was irrelevant for Dim1 and Dim2, was represented in Dim3 and Dim4 (not shown here; see dissertation Ta-

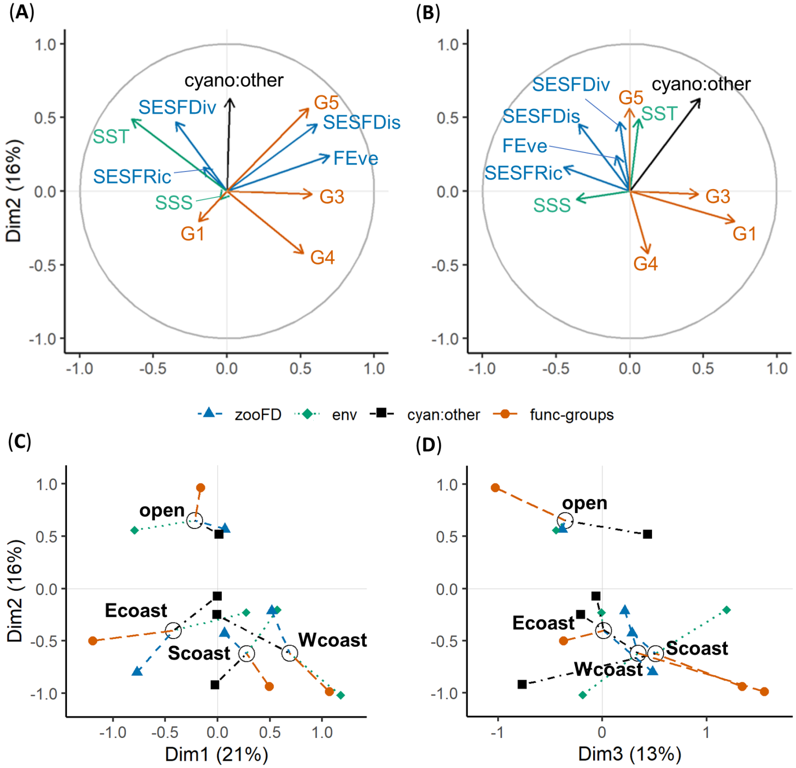


Figure 3.4. **A**,**B**) Environmental gradients in the Gulf of Riga represented as a correlation circle and (**C**,**D**) environmental characteristics within each study area: open–open water area; Ecoast–eastern coastal area; Scoast–southern coastal area; Wcoast–western coastal area. Subgraphs (**A**,**C**) show results for Dim1 and Dim2; subgraphs (**B**,**D**) show results for Dim3 and Dim2. The percentage variability of the data set represented by dimensions are shown in parenthesis. Colours indicate grouping of variables. zooFD (mesozooplankton functional diversity indices): SESFRic, FEve, SESFDiv, and SESFDis; env (environmental abiotic factors): SST–surface (0–10 m) temperature, SSS–surface (0–10 m) salinity; cyan:other (cyanobacteria-to-other phytoplankton biomass ratio); func-groups (mesozooplankton functional groups) as defined in Table 2.2. Figure from Labuce *et al.* (2021).

ble 4.3.). Salinity was negatively correlated to abundance of herbivorous filter-feeders (func.group G1) and large-sized omnivores (func.group G3) (Figure 3.4).

The ensemble of mesozooplankton FD indices showed increased values in open waters compared to coastal areas (Figure 3.4.C,D), except SESFRic, which contributed weakly to the first two MFA dimensions (<2%). Abundances of the G1 and G3 functional groups were negatively correlated with SESFRic (Figure 3.4B). Indices FEve and SESFDis contributed to Dim1 (19.4% and 15.0%, respectively), which related to temperature gradient. SESFDiv and SESFDis were significant factors for Dim2 (11.5% and 10.7%, respectively) indicating an increase in mesozooplankton functional divergence and dispersion towards open waters.

3.4.2. *Coastal waters*

Characteristics of mesozooplankton FD and other environmental factors (Figure 3.4) were similar between all coastal areas. Slight differences were observed along Dim1, respectively, abundance of G3 functional group increased towards western area, while higher values of SST were observed in eastern regions (Figure 3.4A,C).

Despite the high number of detected statistically significant relationships explaining variability of FD dynamics (14 in total), only three of them demonstrated acceptable predictive ability (nrmse $\approx$<1.0; Figure 3.4A,H,I), whereas several more showed moderate results (nrmse up to $\approx$2.0; Figure 3.5B,D-G,L,N). Consequently, only those relationships are regarded as causal links; the other observed relationships may be the result of co-variance or randomness.

The coastal areas of the Gulf of Riga are highly impacted by wind and other coastal disturbances, and thus can be defined as profoundly fluctuating habitats, conversely to open waters. The high freshwater impact also reinforces mixing and turbulence in the area. Riverine discharge is spread along with the eastern and western coastal areas almost equally during summer (Lips *et al.*, 2016). Most likely, physical factors are the features behind the identified similarities between the studied coastal sites and their differences to open waters (Figure 3.4).

Environmental filtering is particularly pronounced in dynamic and fluctuating waters, yet it has been demonstrated that they are also highly productive habitats with effective food webs and intensive biotic interactions (Snoeijs-Leijonmalm, 2017). The majority of identified relationships between coastal mesozooplankton FD and environmental drivers were responses to biotic parameters. The only exception was functional evenness (FEve) that showed a significant (p = 0.0074) and accurate (nrmse = 1.26) negative relationship to abiotic conditions, namely, SST (Figure 3.5G). A decrease in the balance of the filled niche space of the mesozooplankton community (described by FEve) with increasing temperature is a direct manifestation of abiotic filtering under the fluctuation of seasonal forcing. The benefits from warmer or colder conditions differ between mesozooplankton species, consequently creating shifts in species and trait occurrences (e.g., Forster and Hirst, 2012; Kenitz *et al.*, 2017).

The coastal waters of the Gulf of Riga are dominated by herbivorus filter-feeders (func. group G1), including *Keratella* and *Bosmina* species and small omnivores (func.

group G4), which comprise rotifers of the genus *Synchaeta* and Copepoda nauplii (Figure 3.2A). Helenius *et al.* (2017) reported lower zooplankton FD based on feeding traits (similar as in this study) at sites where *Keratella* rotifers or Copepoda nauplii were prevailing, coinciding with the findings of this dissertation (FD is lower in coastal areas where Copepoda nauplii and rotifers prevail).

The long-term dynamics of mesozooplankton functional group abundances (Figure 3.2) clearly showed the differences between coastal and open water systems. Small-sized organisms (func.groups G1 and G4) were more abundant in coastal waters. Body size is considered a master trait that defines the main physical abilities and constraints of an organism (Kiørboe *et al.*, 2018), including its power to retain horizontal and vertical position in the water mass (increasing with size) (McManus and Woodson, 2012).

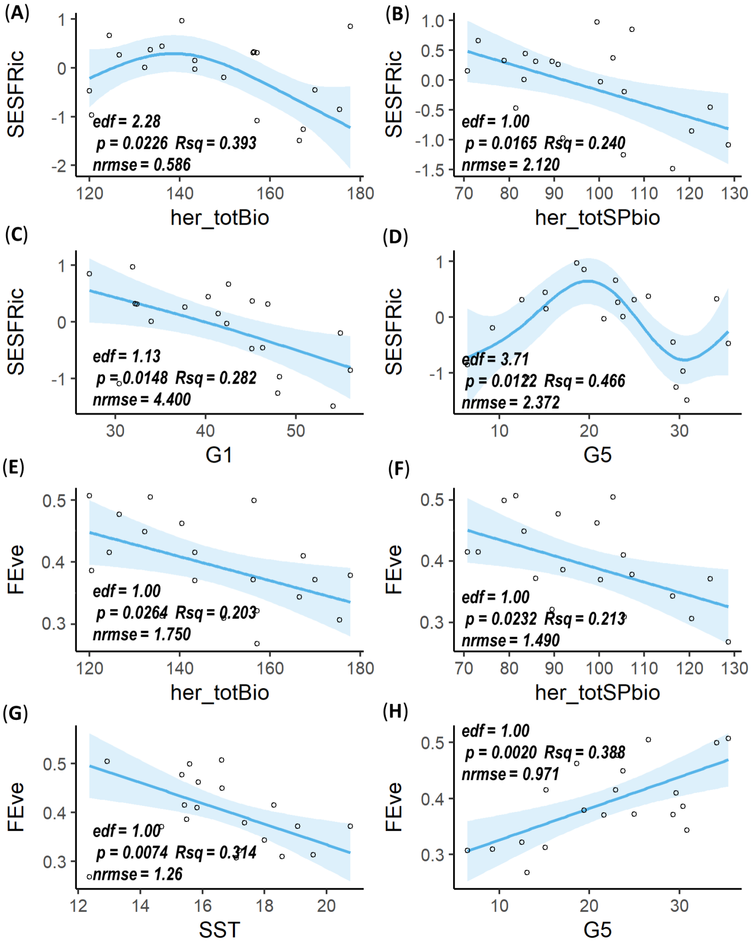


Figure 3.5. Continued in the next page. Figure from Labuce *et al.* (2021).

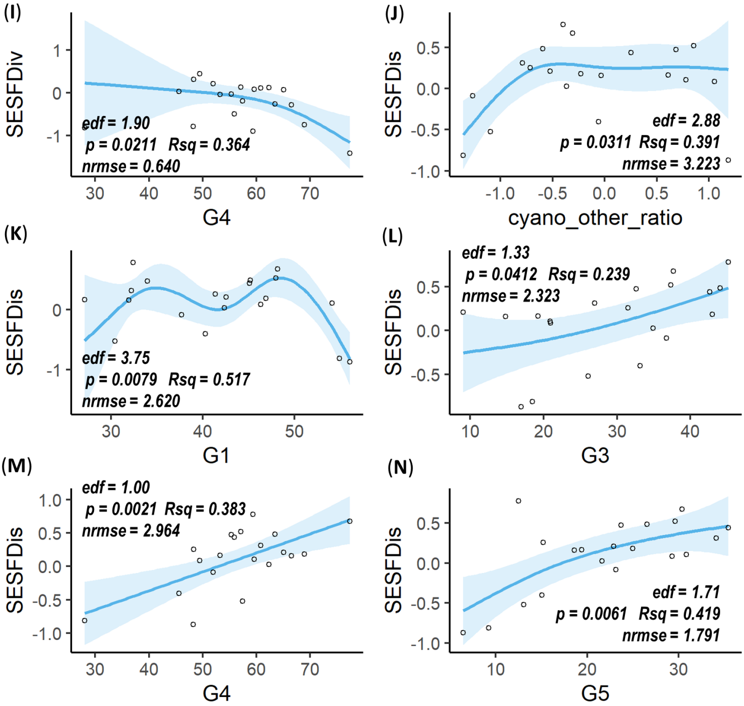


Figure 3.5. Response curves from GAM based on train data (1993–2014) of the Gulf of Riga coastal waters. Only models with $p \leq 0.05$ are shown. (**A–D**) show responses to environmental drivers of SESFRic (functional richness), (**E–H**) FEve (functional evenness), (**I**) SESFDiv (functional divergence), and (**J–N**) SESFDis (functional dispersion) indices. edf–estimated degrees of freedom for the model terms; *p*–the *p* value for the smoothing term Rsq (adjusted R-squared); nrmse–absolute values of the root mean square error normalised by the standard deviation, based on test data (2015–2017). her_totBio-total–herring biomass, 1000 tonnes; her_totSPbio–herring spawning biomass, 1000 tonnes; cyano_other_ratio–cyanobacteria-to-other phytoplankton biomass ratio, box-cox transformed; G1–G5-abundance of group G1–G5, box-cox transformed; SST-sea surface temperature, C°. Figure from Labuce *et al.* (2021).

Plausibly, the aggregation of non-migrating small-size taxa in the water column is also supported by enhanced jet-like currents that are present in the Gulf of Riga within western and eastern coastal areas during the summer period (Lips *et al.*, 2016). Kahru *et al.* (1986) have analysed physical-biological coupling in frontal structures in the Baltic Sea. They found indeed small-sized zooplankters, namely *Bosmina* and *Synchaeta*, as dominating taxa in the fronts and noted the increased zooplankton abundances in the regions, which was explained by particle aggregations due to flow convergence. However, only a focused study on the physical processes and their biological implications within the above-mentioned currents of the Gulf of Riga would give more profound information.

The majority of the taxa within groups G1 and G4 have short life cycles (except for Copepoda nauplii and meroplankton that are ephemeral development stages) and the ability of parthenogenetic reproduction (rotifers, cladocerans), which allows for rapid development under suitable conditions and consecutive triumph in competitive encounters Winder and Varpe (2020). The dominance of one group affects the evenness of mesozooplankton population thus reduces the value of FEve index (Carmona *et al.*, 2016). The abundance of group G4 negatively affected functional divergence (SESFDiv) of the mesozooplankton community (Figure 3.5I). Functional divergence has been identified as a descriptor for niche differentiation, thus resource availability and competition within a filled trait space (Mason *et al.*, 2005). Therefore, the identified negative relationship builds up to the reason that the competition over resources is a significant driver for the mesozooplankton FD in the coastal Gulf of Riga, especially at times when a rapidly-developing functional group dominates the community.

3.4.3. *Open waters*

In open waters, herring recruitment and spawning biomass demonstrated contradicting relation to FEve index (Figure 3.6B,C). Increasing herring recruitment had a positive correlation with FEve, whereas increasing spawning biomass had a negative one. The opposing impacts were unexpected, yet, it can be explained by the broader scope of prey available for adult herring compared to younger fish (Arrhenius and Hansson, 1993) resulting in more targeted feeding on the G5 mesozooplankton functional group (Livdāne *et al.*, 2016; Arrhenius and Hansson, 1993). In other words, adult herring prey upon larger copepods and cladocerans only and will switch to other prey such as mysids or amphipods if the preferred zooplankton are in sub-optimal densities (Arrhenius and Hansson, 1993). Moreover, FEve correlated to the abundance of large-sized omnivores (func.group G5; the main prey for adult herring) in the open waters of the Gulf of Riga (Figure 3.6D), indicating that the increase of individuals from G5 group balances the diversity of the mesozooplankton population. Conversely, young herring tend to be less capable of switching prey (Arrhenius and Hansson, 1993), hence affect mesozooplankton population more evenly. Albeit, considering that the main feeding grounds for the Gulf of Riga herring larvae and young fish are coastal areas (Arula *et al.*, 2012; Ojaveer, 2017), most likely, number of herring recruitment does not directly affect mesozooplankton FD in the open waters of the Gulf of Riga. The detected relationship (3.6B) could be a result of cross-relations between analysed parameters.

Similarly as in the coastal areas, the variation of SESFDiv index could not be explained by the environmental factors included in the analysis; SESFDiv did not show any statistically significant correlation in open waters. SESFDis, on the other hand, depended on the distribution of functional groups (Figure 3.6E-G), although *nrmse* of the observed correlations was greater than 1, therefore it was not deemed as a causal relationship, but rather as a co-variance.

3.5. Effects of benthic-derived recruitment on mesozooplankton FD

The results of hatching experiments show the direct bentho-pelagic coupling effects on mesozooplankton community (Figure 3.7). Individuals of two functional groups

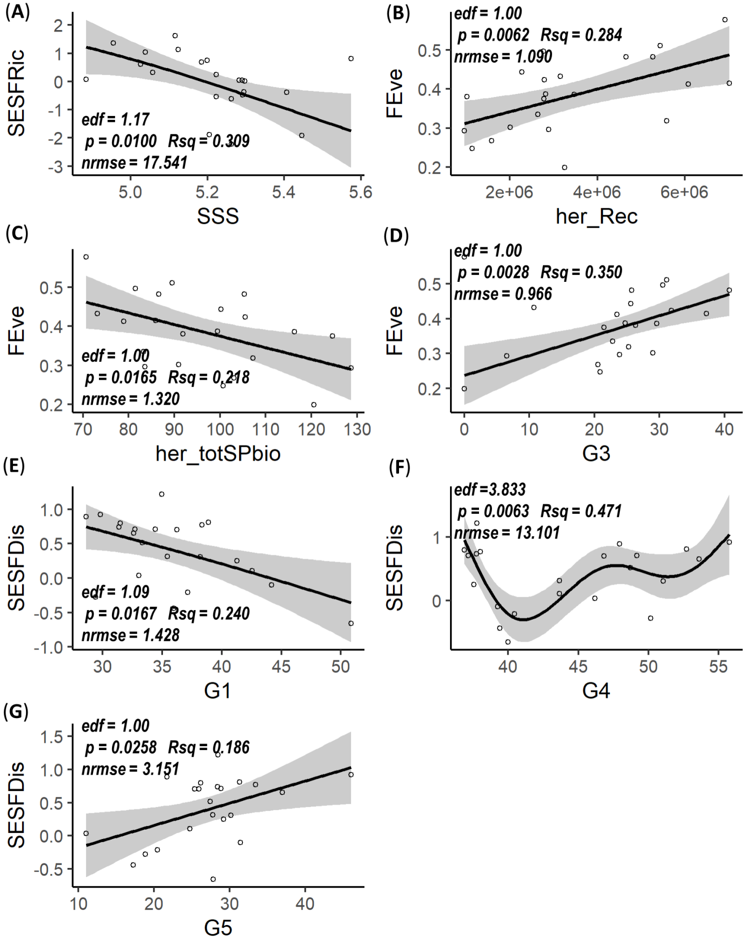


Figure 3.6. Response curves from GAM based on test data (1993–2014) of the Gulf of Riga open waters. Only models with p≤0.05 are shown. (**A**) show responses to environmental drivers of SESFRic (functional richness), (**B–D**) FEve (functional evenness), and (**E–G**) SESFDis (functional dispersion) indices. Statistics as in Figure 3.5. her_Rec–herring recruitment, 1000 ind; her_totSPbio–herring spawning biomass, 1000 tonnes; G1–G5-abundance of group G1–G5, box-cox transf.; SST-sea surface salinity, PSU. Figure from Labuce *et al.* (2021).

(G1, G4) hatched from the sediments. The vast majority of hatchlings were small-sized omnivores (G4 func.group), i.e., *Acartia* nauplii, that grow into large-sized omnivores (G3 func.group). Hence processes in benthic habitat can directly impact benthic-derived recruitment for small- and large-sized omnivores, and, at a lesser degree, also herbivorous filter-feeders (G1 func.group).

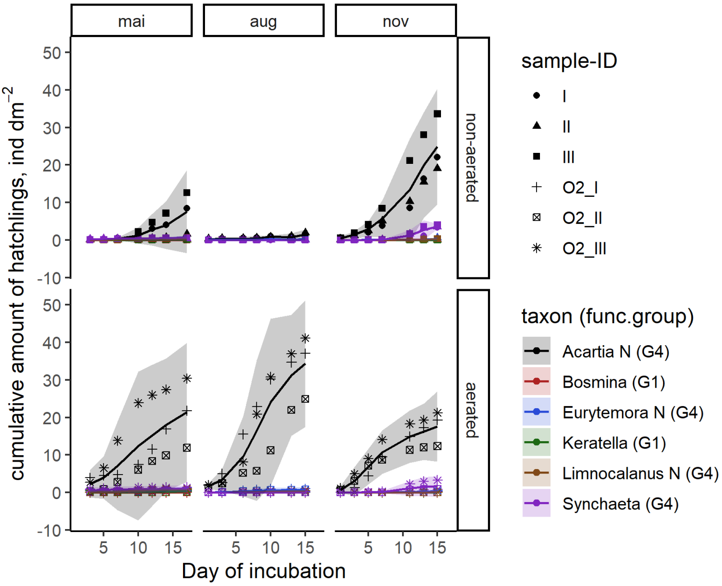


Figure 3.7. Zooplankton hatchlings from upper 2 cm layer of sediments collected in the Gulf of Riga (station 121A). Individuals grouped according taxonomic affiliation. Incubation conducted in 2018. G1, G4 - functional guild of mesozooplankton as defined in Table 2.2.

Water turbulence and air supply during incubation were controlled. Significantly more benthic eggs hatched from the samples with air supply (Figure 3.7), indicating that under strong stratification conditions, benthic-derived recruitment of mesozooplankton may be reduced or stopped. The minimal oxygen concentration that ensures the survival of Copepoda eggs is 0.18 mL L^{-1} (Katajisto, 2004). An oxygen conditions frequently observed in the demersal layer of the deepest regions of the Gulf of Riga (LHEI database). According to the latest projections, stratification will enforce in the Gulf of Riga under climate change (Von Storch *et al.*, 2015) potentially exacerbating oxygen conditions and the resulting effects.

3.6. Synopsis: functional diversity of brackish zooplankton – causes and effects

Zooplankton are an intermediary component in the pelagic food web, hence its FD is expected to be affected by both bottom-up and top-down control. However, causal effects from lower levels (i.e., cyanobacterial dominance) were not identified. Overall, impacts from higher trophic levels (herring), intra-group interactions (at zooplankton level), and abiotic factors were recognized (Figure 3.8).

The influence of abiotic factors on zooplankton FD is most pronounced in the ”coastal-to-open water” spatial gradient. The coastal areas are homogeneous habitats along the vertical dimension (depth) due to weak stratification that is easily disruptable by rapidly changing physical conditions (e.g., winds, upwelling, runoff). Under these conditions, short-lived organisms with high reproductive rates thrive. Subsequently, certain functional groups with similar traits predominate in the coastal areas, reducing zooplankton FD and mean zooplankter size that in turn negatively affect the food quality of planktivorous fish. In dense population conditions, intra-group competition (for functionally similar species) and niche differentiation (for functionally different species) are decisive for the co-existence of species (Prati *et al.*, 2021). Given the homogeneity along the vertical gradient and associated limited niche differentiation in coastal areas, the main determining factor for zooplankton diversity there is intra-group competition, resulting in the thriving of r-strategists (func.groups G1, G4) that are specially adapted to fast niche occupation.

In open waters, a pronounced stratification is present during summer providing different niches (upper warm layer, thermocline, deeper cool layer), resulting in an increased number of species as well as higher FD of zooplankton (Figures 3.1 and 3.4) (see also Schulz *et al.*, 2012). SESFDis and SESFDiv values are higher in open waters compared to coastal areas. Mason *et al.* (2005) noted that an increase in SESFDiv index implies available and free niche space within the habitat, indirectly indicating lowered competition. Niche differentiation allows distinct functional groups to co-exist in the same habitat. For example, in the Gulf of Riga, functional group G5 increased in numbers toward open waters. Intra-group predation can also control the prevalence of small-sized, rapidly reproducing organisms, lowering the population density and easing the intra-group competition. Functional group G5 includes predatory taxa, thus the deduced free niche space in open waters of the Gulf of Riga might be a result of both – niche differentiation and intra-group predation. Moreover, herring, the main planktivorous fish in the region, selectively feeds on functional group G5 (Livdāne *et al.*, 2016), controlling its predatory pressure on lower trophic zooplankton groups.

Benthic-derived recruitment is especially important to small- (func.group G3) and large-sized omnivores (func.group G4), and, to a lesser degree, also to herbivorous filter-feeders (G1 func.group). As well as the predatory *C.pengoi*, although hatching from benthic eggs was not observed in this study, and other cladocerans are known to overwinter in the benthic habitat in a form of resting eggs (Marcus, 1990; Sopanen, 2008). One of the threats to benthic-derived recruitment is the decrease in oxygen concentration in the demersal layer, which would affect above-mentioned functional groups, significantly reducing their recruitment.

In conclusion, the functional diversity of zooplankton is controlled by abiotic factors, as they form a pelagic habitat, but biotic factors and interactions between organisms and functional groups are equally important in shaping functional diversity. Biotic factors can selectively affect specific functional groups, hence directly impacting the functioning of the trophic food web. In future studies, it would be useful to explore the relationship between FD indices for each trophic level and food web characteristics, as well as to describe coastal pelagic processes in more detail. Korpinen *et al.* (2022) emphasized the need to link environmental indices and indicators through ecosystem models to better understand interactions between trophic levels, resulting in more accurate assessments of food webs and habitats.

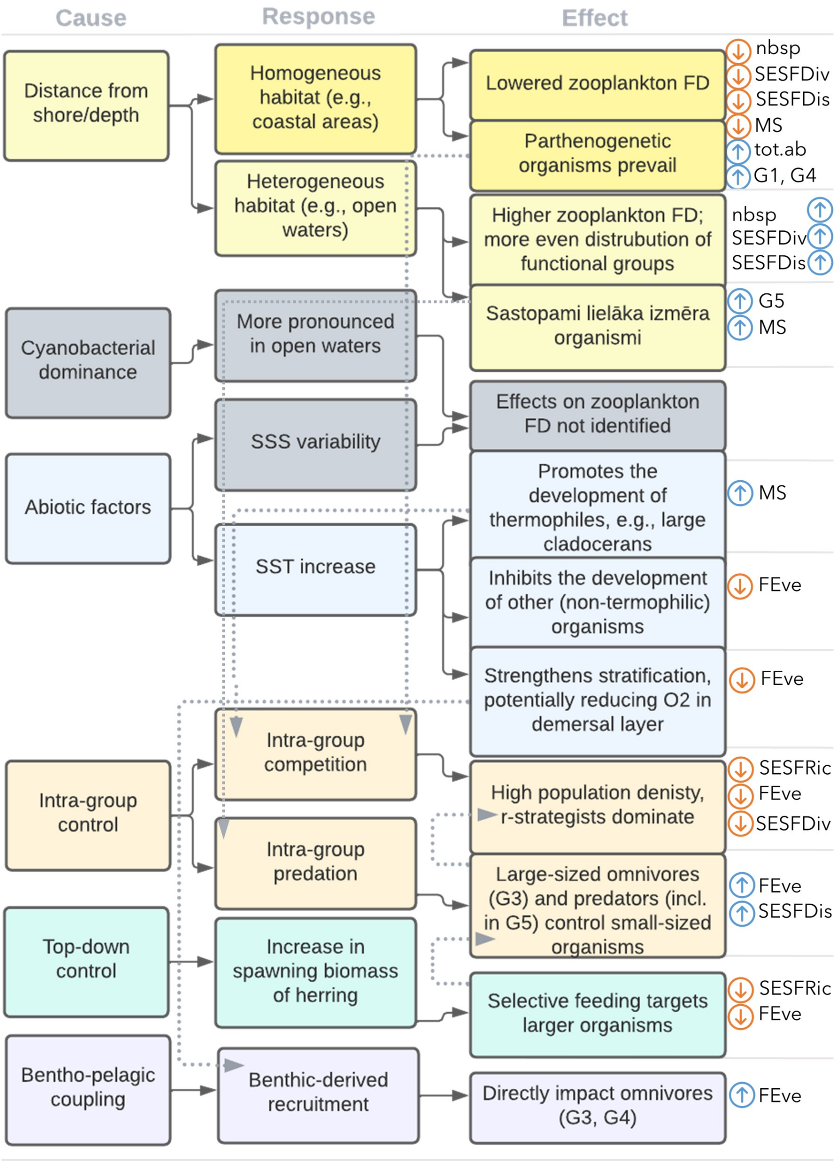


Figure 3.8. Observed effects of environmental factors on zooplankton functional diversity (FD) metrics. Solid arrows indicate a direct effect; dotted arrows – an indirect effects (the most significant ones are indicated). nbsp–number of species; SESFRic, SESFDiv, SESFDis, FEve–FD indices; MS–mean zooplankter size; tot.ab–total zooplankton abundance (stock); G1–G5–functional groups of mesozooplankton (see Table 2.2); SST–sea surface 0-10 m layer mean temperature; SSS–sea surface 0-10 m layer mean salinity.

4. CONCLUSIONS

- The list of *Synchaeta* species in the Baltic Sea is incomplete, potentially underestimating the taxonomic diversity. Additional attention to *Synchaeta* identification at species-level is required in future studies, including both electron microscopy for trophi analysis and molecular methods for accurate species identification.
- In the five years since the first discovery of non-indigenous copepod *Eurytemora carolleeae*, it has failed to establish a settled population in the Gulf of Riga. However, considering the high reproductive rates and a longer life expectancy of *E.carolleeae*, the accurate identification of *Eurytemora* species should continue to receive increased attention in the region.
- MSTS indicator describes the environmental status of the pelagic habitat in the open waters of the Gulf of Riga. Adaptations to the methodological approach are needed to assess coastal waters. Given that coastal waters are typical feeding grounds for herring larvae and they feed on small organisms, the recommendation is to include only the total stock (TS) parameter, more precisely the total zooplankton abundance (TZA).
- The functional diversity of mesozooplankton is primarily controlled by abiotic factors if the habitat is homogeneous along the vertical dimension (as observed in the coastal waters of the Gulf of Riga); the functional diversity of mesozooplankton is primarily controlled by biotic factors, if the habitat is heterogeneous – different abiotic factors divide the habitat into several niches or micro-habitats (as observed in the open waters of the Gulf of Riga).
- The functional diversity of mesozooplankton was lower in the coastal waters of the Gulf of Riga than in open waters. This difference can be explained by the domination of herbivorous filter-feeders and small-sized omnivores. Both of these functional groups contain taxa able to reproduce parthenogenetically, thus rapidly forming high numbers in volatile and dynamic abiotic conditions typical in the coastal waters.
- Individuals from two functional groups (G1–herbivorous filter-feeders, G4–small-sized omnivores) hatched from the sediments. Hatching activity was observed in spring, summer and autumn samples. Noticeably higher amounts of benthic eggs hatched in water-aerated samples, indicating that under stratification conditions, due to reduced oxygen concentration, egg hatching activity is adversely affected, which may directly impact G1 and G4 recruitment, lowering their abundance in pelagic habitat and shifting overall mesozooplankton functional diversity.
- Characteristics of mesozooplankton functional diversity provide information on mesozooplankton population structure, allowing evaluation of the underlying processes, thus demonstrating the ecological importance of functional diversity metrics and their practical application in ecological studies.

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